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ments is to increase the concentrations of the salts in the cells of the tissue.

On Certain Asymptotic Expressions in the Theory of Linear Differential Equations: W. E. Milne, Department of Mathematics, Bowdoin College. Formulas more precise than those previously obtained by Birkhoff are given.

On Newton's Method of Approximation: Henry B. Fine, Department of Mathematics, Princeton University. A condition is given under which Newton's method of approximation for computing a real root of an equation, and the extension of this method used in computing a root of a system of equations, will with certainty lead to such a root or solution.

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SPECIAL ARTICLES

THE FUNCTION OF THE APYRENE SPERMATOA

SINCE the discovery of the dimorphism of spermatozoa in *Paludina* by von Siebold, 1836, numerous biologists have worked with this strange phenomenon without being able to find a conclusive explanation. On the one side investigators were found, like v. Brunn, who regarded the abnormal type of spermia as abortive elements without any function, whereas others, like Brock and Auerbach, thought it impossible that such typical elements could be produced regularly without being functional. It is well known how a new basis was given to these discussions, when Meves (1903)¹ worked out the details of the spermatogenesis of these two types of spermatozoa. He first proved that the atypical spermia in Prosobranchs contain only a small part of the chromatin of the cell and called them *oligopyrene* spermatozoa. He further discovered a similar dimorphism in some moths, but here the atypical spermia contain no chromatin at all, they are apyrene. Meves

¹ Meves, F., "Ueber oligopyrene und apyrene Spermien und ueber ihre Entstehung nach Beobachtungen an *Paludina* und *Pygaera*," *Arch. Mikr. Anat.*, 61, 1903. See there the quotations of the previous literature.

could get no evidence regarding the possible function of these elements, but he felt sure that they must have some function and pointed to the possibility of a fertilization by these elements, which would be interpreted as an "Entwicklungserregung." Since then much morphological work upon the structure and development of the atypical elements has been done, especially by Retzius, Kuschakewitsch, Reinke,² which, however, does not interest us here.

The interest in the possible function of these elements was awakened again, when the facts about the sex-chromosomes became known and their relation to the other kind of dimorphism of spermatozoa in insects and the mechanism of sex inheritance. The idea was promoted by R. Hertwig³ that this dimorphism might also be connected with sex-determination and he tried to fit these possibilities into his general ideas of sex-determination, considering the possibility of fertilization by apyrene spermatozoa as a kind of male-producing parthenogenesis. These ideas were the starting point of some work which Popoff⁴ did with *Paludina*. But he was unable to prove that the oligopyrene spermatozoa of that snail take any part in fertilization, although they are found in sufficient numbers in the oviduct. The only positive result was that in impregnated snails the oligopyrene spermia degenerate and die much earlier than the normal ones. Lams,⁵ who later studied the fertilization of *Murex*, was also unable to find any such spermatozoon inside the egg. On this point we have only a single positive observa-

² Retzius, G., *Biol. Unters.*, N. F., Vol. 12, 13, 14, 1905-1909. Kuschakewitsch, S., "Studien über den Polymorphismus der männlichen Geschlechtselemente bei den Prosobranchia," *Arch. Zellforschg.*, 10, 1913 (complete literature). Reinke, E. E., "The Development of the Apyrene Spermatozoa of *Strombus tuberculatus*," Publ. 183, Carnegie Inst., Washington, 1914.

³ Hertwig, R., "Ueber Correlation von Zell- und Kerngrösse, etc.," *Biol. Centrbl.*, 23, 1903.

⁴ Popoff, M., "Eibildung bei *Paludina vivipara*, etc.," *Arch. mikr. Anat.*, 70, 1902.

⁵ Lams, H., "Recherches concernant le dimorphisme des éléments sexuels chez le *Murex*," *Ann. Soc. Med. Gand.*, 89, 1910.

tion given by Kuschakewitsch.⁶ He found in the eggs of a prosobranch, *Aporrhais*, twenty minutes after fertilization, an oligopyrene spermium besides a typical one. Even taking it for granted that this is not an accident of sectioning, the facts are not yet convincing. And Kuschakewitsch himself is indeed rather skeptical and does not want to draw far-reaching conclusions. It might be mentioned that we had formulated a hypothesis⁷ of sex-determination on the basis of such a process which, however, we have since abandoned. The latest work on these questions, by Reinke (*l. c.*) finally reached one positive, but rather discouraging result. He finds in *Strombus* that the atypical spermatozoa never reach the receptaculum seminis but degenerate and are surrounded by a capsule. The simultaneous work of von Kemnitz⁸ also failed to attain positive results, although the fact is of interest that the hermaphroditic prosobranch *Valvata* exhibits no dimorphism of spermatozoa.

As far as we know, only once has a real experiment been performed to test the function of the apyrene spermatozoa. R. Hertwig⁹ started from the hypothesis that fertilization with apyrene spermia is comparable to the parthenogenesis and produces males. Therefore he crossed two species of moth, *Pygæra andchoreta* and *curtula*, which are known to produce apyrene spermia. If fertilization could occur by these latter sex-cells, the offspring, supposedly the males, ought to exhibit only maternal characters. The results were entirely negative, both sexes in F_1 being intermediate in regard to the characters of the parental species.

⁶ Kuschakewitsch, S., "Zur Kenntnis der sogenannten wurmförmigen Spermien der Prosobranchier," *Anat. Anz.*, 37, 1910.

⁷ Goldschmidt, R., "Kleine Beobachtungen und Ideen zur Zellenlehre," I., *Arch. Zellforsch.*, 1910.

⁸ V. Kemnitz, G., "Beiträge zur Kenntnis des Spermatozoendimorphismus," *Arch. Zellf.*, 12, 1914.

⁹ Hertwig, R., "Ueber den derzeitigen Stand des Sexualitätsproblems, etc.," *Biol. Centrbl.*, 32, 1912.

We are now able to state a few experimental facts in regard to the apyrene spermia of moths which have been noticed in connection with some other work. The first question is are the apyrene spermia able to fertilize an ovum or to cause development? Some answer is given by the following facts. In my experiments on intersexuality in the gipsy-moth an almost complete series of intersexual males was produced in 1915 showing every stage from a male to a female. Now up to a certain degree of intersexuality these individuals behave sexually like males and succeed in mating with the females. For many years we have known that such intersexual males of a low grade are completely fertile, and the eggs fertilized by them develop normally. It was of course of extreme importance for our work to breed offspring from the higher grades of intersexual males and they were therefore all mated, obviously to the limiting type, which was still male enough to perform the mating. All matings were certainly normal, as every female laid a normal egg sponge, which is only done after a successful mating. From the eggs fertilized by low-grade intersexual males the normal percentage of caterpillars hatched, as in previous years. But from egg batches, fertilized by somewhat higher intersexual males, only a few caterpillars hatched, the rest of the eggs being unfertilized. The numbers were for four cultures 3, 3, 2, 3 caterpillars, the egg batches containing between 100 and 300 eggs. Finally, in the egg batches laid after mating with the highest type of intersexual male, which was still able to mate, not a single egg developed. Now in studying the sex glands of these males we found that in low grade intersexuality they contained normal sperm bundles, but in the higher forms of intersexuality the entire gonad was filled with giant bundles of apyrene spermatozoa. The intermediate forms, which gave a few fertile eggs, were unfortunately not examined. We think it not unsafe to conclude from these facts that apyrene spermatozoa can not induce development, even if they enter the eggs, which, however, also seems improbable.

But if the atypical spermatozoa play no part in fertilization, what is then their function? We think we can derive an answer from some experiments carried on during the winter of 1914-15 on spermatogenesis in vitro,¹⁰ an answer which is in full harmony with the above quoted results of other investigators.

In rearing the sperm follicles of the moth *Samia cecropia* in tissue-cultures, we found that in the fall the follicles taken from the pupæ finished practically all their normal spermatogenesis and a follicle with apyrene spermatozoa never appeared. But in January and February the results were quite different. The fresh material already contained many degenerating follicles. In the tissue cultures only a very few follicles performed the spermiogenesis, most of them dying after repeated unsuccessful trials to undergo the maturation divisions. These testes, however, already contained many apyrene follicles. Later in February some pupæ were kept in the thermostat for a week. In examining their testes they were found filled with sperm bundles, the great majority of them being apyrene.

In the same experiment it could be shown, further, that the transformation of a sperm-cell into a spermatozoon is caused by the physical condition of the follicle membrane and can be produced artificially to a certain degree. Now one of the main characteristics of the development of the apyrene spermatozoa is the production of caryomerites from the chromosomes and their further degeneration. The same phenomenon has been produced by Conklin¹¹ in the cleavage cells of *Crepidula* by changing the osmotic conditions of the surroundings. Combining these facts, we reach the conclusion that a definite change in the

physical properties of the follicle membrane forces the sperm cells within, physically, to undergo definite atypical changes, which lead to the formation of an apyrene spermium. This process is therefore nothing but the expression of a reaction, necessitated by the physico-chemical properties of the sperm-cell on which the abnormal surroundings act; a reaction produced by abnormal conditions, a teratoma, a *lusus naturæ*. The typical form of the abnormal sex-cells for a given species is as much necessitated by the specific substratum as the typical form of a plant-gall. The apyrene spermatozoon is a functionless reaction-product.

The results derived from the experiments with intersexual animals are in harmony with this conception derived from the study of tissue cultures. It is well known that the chemical properties of the hemolymph in insects change during metamorphosis in connection with histolysis, and the entire metabolism is put on a different basis, as Weinland¹² proved. In the case of the pupæ of *Samia* it is easy to observe, without going into chemical details, that the blood in old pupæ which produce the atypical spermatozoa has very different properties from those in the young. On the other hand, the work of Steche and Geyer¹³ has shown that in the gipsy-moth the chemical characters of the blood are very different in the male and female sex. Hence it might reasonably be expected—tests are going to be made—that in intersexual individuals, where every single character is intermediate to a definite degree between the two sexes, the blood is also different from the normal blood, thus producing in the case of intersexual males those physico-chemical conditions which account for the formation of the apyrene spermatozoa.

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¹⁰ A full account of that piece of work has probably appeared meanwhile in the *Arch. f. Zellforschung*, 1916, under the title: "Einige Versuche zur Spermatogenesis in Vitro." A preliminary notice is found in *Proc. Nat. Ac. Sc.*, I, 1915.

¹¹ Conklin, E. G., "Experimental Studies on Nuclear and Cell-division in the Eggs of *Crepidula*," *Jour. Ac. Sc.*, 15, 1912.

¹² Weinland, E., "Ueber die Stoffumsetzungen während der Metamorphose der Fleischfliege," *Ztschr. f. Biol.*, 47, 1906.

¹³ Geyer, K., "Untersuchungen über die chemische Zusammensetzung der Insectenhaemolymph," *Ztschr. wiss. Zool.*, 105, 1913.